organizer of cell polarity that limits the escape of PINs from polar domains. On the other hand, one cannot exclude somewhat more indirect consequences of disrupting either microtubule arrays or cellulose fibrils on PIN localization. Microtubule arrays play a central part in the orderly positioning of proteins whereas highly pleiotropic phenotypes associated with cellulose synthase mutants are likely a consequence of quite a range of defects that eventually may result in an altered positioning of the PINs [13,20].

These are fascinating questions for future studies that should lead to exciting insights, connecting dynamic polarity changes in plant cells and tissues to the static plant cell wall. Undoubtedly, this recent work will have strong implications for our current models on perception of and adaptation to environmental cues for plants.

References

1. Friml, J. (2010). Subcellular trafficking of PIN auxin carriers in auxin transport. Eur. J. Cell Biol. *89*, 231–235.
2. Kleine-Vehn, J., and Friml, J. (2008). Polar targeting and endocytic recycling in auxin-dependent plant development. Annu. Rev. Cell Dev. Biol. *24*, 447–473.
3. Tanaka, H., Kitakura, S., De Rycke, R., De Groodt, R., and Friml, J. (2009). Fluorescence imaging-based screen identifies ARF GEF component of early endosomal trafficking. Curr. Biol. *19*, 391–397.
4. Geldner, N., Anders, N., Wolters, H., Keicher, J., Kornberger, W., Muller, P., Delbarre, A., Ueda, T., Nakano, A., and Jürgens, G. (2003). The Arabidopsis GNOM ARF-GEF mediates endosomal recycling, auxin transport, and auxin-dependent plant growth. Cell *112*, 219–230.
5. Abas, L., Benjamins, R., Malenica, N., Paciorek, T., Wiśćniewska, J., Moulinier-Anzola, J.C., Sieberer, T., Friml, J., and Luschnig, C. (2006). Intracellular trafficking and proteolysis of the Arabidopsis auxin-efflux facilitator PIN2 are involved in root gravitropism. Nat. Cell Biol. *8*, 249–256.
6. Michniewicz, M., Zago, M.K., Abas, L., Weijers, D., Schweighofer, A., Meskiene, I., Heisler, M.G., Ohno, C., Zhang, J., Huang, F., *et al*. (2007). Antagonistic regulation of PIN phosphorylation by PP2A and PINOID directs auxin flux. Cell *130*, 1044–1056.
7. Dhonukshe, P., Huang, F., Galvan-Ampudia, C.S., Mähönen, A.P., Kleine-Vehn, J., Xu, J., Quint, A., Prasad, K., Friml, J., Scheres, B., *et al*. (2010). Plasma membrane-bound AGC3 kinases phosphorylate PIN auxin carriers at TPRXS(N/S) motifs to direct apical PIN recycling. Development *137*, 3245–3255.
8. Huang, F., Zago, M.K., Abas, L., van Marion, A., Galvan-Ampudia, C.S., and Offringa, R. (2010). Phosphorylation of conserved PIN motifs directs ArabidopsisPIN1 polarity and auxin transport. Plant Cell *22*, 1129–1142.
9. Zhang, J., Nodzynski, T., Pencík, A., Rolcík, J., and Friml, J. (2010). PIN phosphorylation is sufficient to mediate PIN polarity and direct auxin transport. Proc. Natl. Acad. Sci. USA *10*, 918–922.
10. Men, S., Boutté, Y., Ikeda, Y., Li, X., Palme, K., Stierhof, Y.-D., Hartmann, M.-A., Moritz, T., and Grebe, M. (2008). Sterol-dependent endocytosis mediates post-cytokinetic acquisition of PIN2 auxin efflux carrier polarity. Nat. Cell Biol. *10*, 237–244.
11. Feraru, E., Feraru, M.I., Kleine-Vehn, J., Martinière, A., Mouille, G., Vanneste, S., Vernhettes, S., Runions, J., and Friml, J. (2011). PIN polarity maintenance by the cell wall in Arabidopsis. Curr. Biol. *21*, 338–343.
12. Wiśćniewska, J., Xu, J., Seifertova, D., Brewer, P.B., Ruzicka, K., Blilou, I., Rouquie, D., Benkova, E., Scheres, B., and Friml, J. (2006). Polar PIN localization directs auxin flow in plants. Science *312*, 883.
13. Pilling, E., and Hoefte, H. (2003). Feedback from the wall. Curr. Opin. Plant Biol. *6*, 1–6.
14. Keegstra, K. (2010). Plant cell walls. Plant Physiol. *154*, 483–486.
15. Liepman, A.H., Wightman, R., Geshi, N., Turner, S.R., and Scheller, H.V. (2010). Arabidopsis – a powerful model system for plant cell wall research. Plant J. *61*, 1107–1121.
16. Boutté, Y., Crosnier, M.-T., Carraro, N., Traas, J., and Satiat-Jeunemaitre, B. (2006). The plasma membrane recycling pathway and cell polarity in plants: studies on PIN proteins. J. Cell Sci. *119*, 1255–1265.
17. Heisler, M.G., Hamant, O., Krupinski, P., Uyttewaal, M., Ohno, C., Jönsson, H., Traas, J., and Meyerowitz, E. (2010). Alignment between PIN1 polarity and microtubule orientation in the shoot apical meristem reveals a tight coupling between morphogenesis and auxin transport. PLoS Biol. *8*, e1000516.
18. Paredez, A.R., Somerville, C.R., and Ehrhardt, D.W. (2006). Visualization cellulose synthase demonstrates functional association with microtubules. Science *312*, 1491–1495.
19. Lloyd, C., and Chan, J. (2008). The parallel lives of microtubules and cellulose microfibrils. Curr. Opin. Plant Biol. *11*, 641–646.
20. Buschmann, H., and Lloyd, C.W. (2008). Arabidopsis mutants and the network of microtubule-associated functions. Mol. Plant *6*, 888–898.

Department of Applied Genetics and Cell Biology, University of Natural Resources and Life Sciences, Vienna, Muthgasse 18, 1190 Wien, Austria.
E-mail: barbara.korbei@boku.ac.at, christian.luschnig@boku.ac.at

DOI: 10.1016/j.cub.2011.01.062

Climbing Plants: Attachment and the Ascent for Light

How do vines climb upward and harvest sunlight? A detailed study of one species (*Galium aparine* L.) shows that leaf hairs (trichomes) provide one solution that solves both tasks simultaneously.

Karl J. Niklas

Charles Darwin sorted climbing plants into five categories based on their type of attachment mechanism (i.e., hook-climbers, twining plants, leaf-climbers, tendril-bearers, and root-climbers) [1]. Based on his detailed studies, Darwin speculated that climbers evolved "in order to reach the light with wonderfully little expenditure of organized matter, in comparison with trees [that] support a load of heavy branches [with] a massive trunk" [1]. Accordingly, he hypothesized that climbing plants steal sunlight from their host plants by virtue of being mechanical parasites. This supposition accords well with a recent study published in the *Proceedings of the Royal Society B* [2] showing that the climbing weedy species *Galium aparine* produces leaves with hooked hairs that allow it to climb up neighboring plants and assure that its leaves preferentially shade those of the plants that provide it mechanical support.

Previous research has shown that the type of attachment mechanism determines the extent to which a climbing species mechanically parasitizes neighboring vegetation [3–5]. For example, plants producing tendrils with secretory adhesive pads (e.g., *Parthenocissus tricuspida*) can cling to broad tree trunks or even a building wall (Figure 1), whereas the tendrils of other species lacking adhesive pads (e.g., *Clematis virginiana*) can cling only to narrow stems or trellises. Research has also shown that the type of attachment mechanism significantly affects the successional distribution and ecology of vines and lianas [6] as well as the extent to which mechanical demands change over the lifetime of a climber [6,7]. For example, loosely fixed hook-climbers experience relatively large mechanical stresses and thus typically have comparatively stiff stems, presumably to prevent loosely attached stems from becoming

Figure 1. Growth habit of *Parthenocissus tricuspida* showing old and new growth of a single individual.

unhooked. Indeed, many facultative and semi-self-supporting climbers, which lean on their surrounding vegetation, are also hook-climbers.

However, until recently, little was known directly about attachment mechanisms that permit climbing plants to directly steal sunlight from their host plants. This gap in knowledge has been closed by a detailed anatomical and biomechanical investigation of the herbaceous weedy species *G. aparine* (Figure 2A). Originally classified by Darwin as a hook-climber by virtue of the multicellular prickle-like structures that develop on the petioles and stem ridges of this species (Figure 2B), Bauer *et al.* [2] have now demonstrated that this climbing plant attaches to the surfaces of other plants mainly by adaptations of its leaf laminae, which are covered by hooked unicellular hairs (trichomes). Although hairs are produced on both leaf surfaces, those on the lower (abaxial) leaf surface are curved toward the leaf base in the proximal direction and are situated exclusively on the leaf midrib and margins (Figure 2C). In contrast, the trichomes on the adaxial leaf surfaces are curved toward the leaf tip in the distal direction and distributed evenly over the entire leaf surface. In addition, these trichomes are lignified. These differences in orientation and cell wall lignification allow the leaves of *G. aparine* to preferentially cling to the upper surfaces of neighboring plants in such a manner that they cover and thus shade the leaves of their host plants.

To understand in detail the mechanism underlying this light-stealing strategy, Bauer *et al.* examined the morphological and mechanical properties of leaf hairs, the frictional properties of entire leaf surfaces, the turgor pressures of different leaf tissues, and the bending properties of leaves in different directions. Their analyses demonstrate that the abaxial and adaxial leaf hairs differ significantly in orientation, distribution, anatomy, and mechanical properties and that the friction properties of leaves depend on the direction of the applied force. The result of these differences is a ratchet-like mechanism in which the abaxial leaf surface provides strong attachment to the leaves of neighboring plants, whereas the adaxial leaf surface slides easily off the underside of the leaves of host plants. In this manner, the leaf trichomes of *G. aparine* function as an attachment mechanism that simultaneously orients leaves advantageously for photosynthesis at the expense of host vegetation.

Wind-induced stem flexure facilitates this ratchet-like mechanism [2]. When

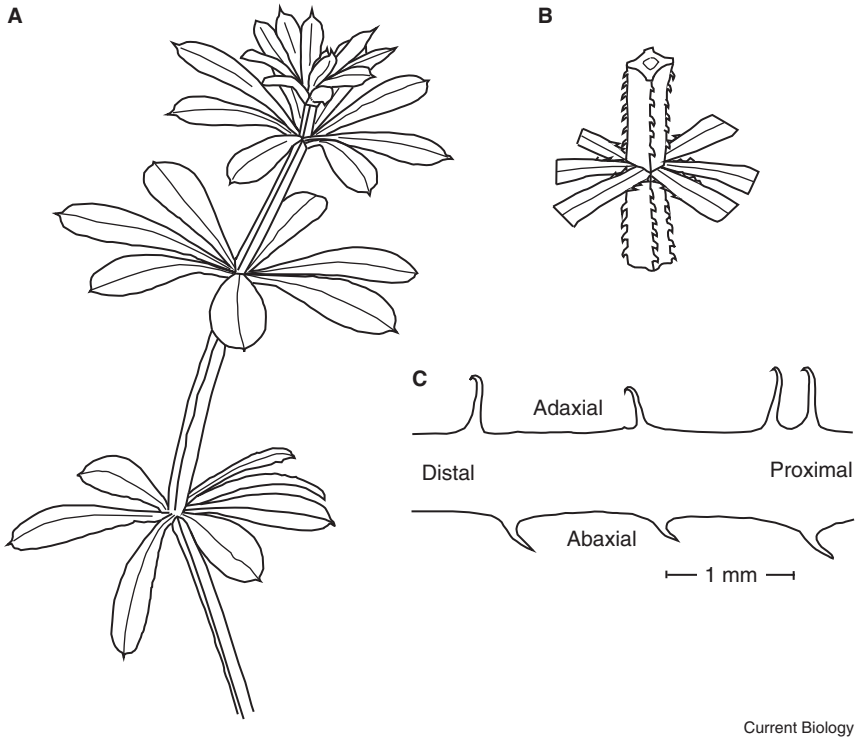

Figure 2. Growth habit and other aspects of *Galium aparine*.

(A) Stem bearing whorls of leaves (petiole and stem hooks not detailed). (B) Stem internode bearing petioles (and distal and proximal sections of adjoining internodes) bearing multicellular hooks. (C) Longitudinal section through leaf lamina with morphologically distinct plant hairs (trichomes) with different orientations with respect to the leaf tip.

the stems of *G. aparine* reach a certain length, they lose mechanical stability and bend under the influence of gravity and wind. Due to the differences in the attributes of abaxial and adaxial leaf surfaces, the action of a mechanical force, such as a gust of wind, moving *G. aparine* toward a neighboring plant results in little friction between connecting leaves. As a result, the leafy shoots of the climber slide into their neighboring vegetation. However, when *G. aparine* is pulled away from its neighboring vegetation, substantial frictional forces are generated between the hairs on the abaxial surfaces of leaves and their interlocking contact surfaces. The opposite happens when *G. aparine* leaves cling with their adaxial surface beneath an adjoining leaf. In this case, the adaxial surface glides easily off contact surfaces while resisting slippage because of the orientation of the adaxial hooks. With this ratchet mechanism acting differently on both leaf surfaces, the leaves of *G. aparine* are preferentially positioned on the leaves of neighboring supporting plants [2].

Unfortunately, Bauer *et al.* [2] did not measure the extent to which *G. aparine* leaves transmit sunlight and thus shade the leaves they overlap. However, the light-response curves of most foliage leaves saturate between 500 and 1000 μmol m^{-2} s^{-1}, which is well below the photon flux of full sunlight (i.e., 2000 μmol m^{-2} s^{-1}) but well above the insignificant amount of light that is transmitted through a typical leaf [8,9]. Had Charles Darwin known about the results reported by Bauer *et al.* [2] he probably would have viewed *G. aparine* as an even more wonderful, albeit insidious example of natural selection.

References

1. Darwin, C. (1865). On the movements and habits of climbing plants. Bot. J. Linnean Soc. *9*, 1–118.
2. Bauer, G., Klein, M.-C., Gorb, S.N., Speck, T., Voigt, D., and Gallenmüller, F. (2010). Always on the bright side: the climbing mechanism of *Galium aparine*. Proc. R. Soc. London. B FirstCite 10.1098/rspb.2010.2038.
3. Putz, F.E. (1984). The natural history of lianas on Barro Colorado Island, Panama. Ecology *65*, 1713–1724.
4. Putz, F.E., and Holbrook, N.M. (1991). Biomechanical studies of vines. In The Biology of Vines, F.E. Putz and H.A. Mooney, eds. (Cambridge: Cambridge University Press), pp. 73–97.
5. Rowe, N.P., Isnard, S., Gallenmüller, F., and Speck, T. (2006). Diversity of mechanical architectures in climbing plants: an ecological perspective. In Ecology and Biomechanics: A Mechanical Approach to the Ecology of Animals and Plants, A. Herrel, T. Speck, and N.P. Rowe, eds. (Boca Raton: CRC press), pp. 35–59.
6. Hegarty, E.E., and Caballé, G. (1991). Distribution and abundance of vines in forest communities. In The Biology of Vines, F.E. Putz and H.A. Mooney, eds. (Cambridge: Cambridge University Press), pp. 313–335.
7. Isnard, S., and Silk, W.K. (2009). Moving with climbing plants from Charles Darwin's time into the 21st century. Am. J. Bot. *96*, 1205–1221.
8. Taiz, L., and Zeiger, E. (2002). Plant Physiology (Sunderland: Sinauer).
9. Niklas, K.J., and Owens, T.G. (1989). Physiological and morphological modifications of *Plantago major* (Plantaginaceae) in response to light conditions. Am. J. Bot. *76*, 370–382.

Department of Plant Biology, Cornell University, Ithaca, NY 14853, USA.
E-mail: kjn2@cornell.edu

DOI: 10.1016/j.cub.2011.01.034